Journal of Research on the Lepidoptera 17(4): 231-239, 1978(80)

Similarities and differences in forewing shape of six California Catocala species (Noctuidae)

John W. Johnson

and

Erich Walter

620 Narcissus Ave., Corona Del Mar, California 92625

Abstract.—The results of a biometrical study of the forewing sizes and proportions of six California species and subspecies of small yellow-winged *Catocala* are presented. Three hundred eighty-four specimens were used. Means of the wing margin lengths and of the ratios of the lengths of the costal, outer and inner margins are compared. The ratios are used to calculate a proportionality product for each of the taxa. The data indicate that the six entities are distinct taxa. On the bases of wing shape and proportion, they can be divided into three distinct groups, supporting previous judgments of similarities between some of the taxa, and placing recently described species in relation to the rest.

Introduction

In California are found six species and, or, subspecies of small yellow-winged Catocalas. They are *Catocala chelidonia* Grote (1881), *Catocala andromache* Henry Edwards (1885), *Catocala mcdunnoughi* Brower (1937), *Catocala andromache* subspecies *benjamini* Brower (1937), *Catocala californiensis* Brower (1976), and *Catocala johnsoniara* Brower (1976). The adults of these taxa resemble each other closely in size, general coloration, and appearance. Barnes and McDunnough (1918) grouped the species then known together. This was done also in the McDunnough checklist (1938). Of interest to the biologist are the relationships of the taxa and the origins of the group. Are they species of diverse origins that have become similar through convergent evolution? If the group is of monophyletic stock, new problems of evolution and speciation arise. The authors have taken as many as four of the six taxa in the same locality in the same night, specifically *andromache andromache, andromache benjamini, californiensis,* and *chelidonia.* At another locality *andromache andromache* and *johnsoniana* are taken together. If the group is monophyletic, what evolutionary mechanisms have facilitated the diversification of the species and maintained the genetic isolation of these sympatric taxa? These questions, in fact, are of central importance to an understanding of the evolution and speciation of the Genus *Catocala* as a whole (Sargent 1976 p. 77 ff.) The six taxa are illustrated in Figure 1.

While the earliest-described species have been known for nearly a century, little has been published about their food plants and immature stages (Barnes and McDunnough 1918 p. 33, Brower 1976 p. 33). With only the adult stages available for comparison little progress has been made toward clarifying their phylogenetic history and relationships. Brower (1937 p. 784) in the species descriptions of *mcdunnoughi* and *benjamini* calls attention to a resemblance between *mcdunnoughi* and *chelidonia*, and assigns *benjamini* to the status of a subspecies under *andromache*. No further comparative studies have been made since.

Beginning about 1930 the authors have collected, observed, and studied the taxa in captivity and in the field. These efforts have yielded significant data on the distributions, flight periods, immature stages, food plants, and aspects of the adult structure other than wing colorations and patterns. From the knowledge that has been gained fresh insights into the relationships of the six taxa soon may be afforded. Reports on our studies of these matters are forthcoming. The present paper describes the results of a study undertaken to seek evidence of the relationships of the taxa by use of structural characteristics other than pattern and color. Using biometrical methods the authors chose, specifically, the size, shape, and proportions of the forewings for a comparative study of the six members of the group.

Procedure

Three hundred eighty-four specimens were used, all field-caught over periods of years, and constituting random sets selected only to the extent of discarding specimens with wings too damaged to allow accurate measurement. Three dimensions were measured on the front wing. The first was the length of the costal margin from the wing base to the distal end of vein Radius 2. The second dimension was the length of the outer margin from the end of vein Radius 2 to the distal end of the 2nd anal vein. The third dimension was the length of the inner margin from the end of the 2nd anal vein to the wing base. The measurements were made on dried, spread specimens under magnification with a set of dividers and read to the nearest half millimeter. The right wing was measured unless damaged required measurement of the left.

Results

Size

In determining the size means of the wing margins for each of the six taxa the means for the two sexes were first obtained and then averaged for the species mean. This was done because one sex, usually the female, was represented in the sample more often than the other.The females tend to be larger in all of the taxa. This would have skewed the species means if the measurements of both sexes had been lumped together. The means of the six taxa may be compared in Table 1.

The means show a progression in size from *chelidonia,* the smallest species, to *johnsoniana,* the largest. While *johnsoniana* and *andromache andromache* fly together in central California, and *chelidonia, californiensis, andromache andromache,* and *andromache benjamini* may be taken in one locality in southern California, yet the population of each taxon has a characteristic mean size of the forewings distinct from that of the others with which it may be associated. These differences in size clearly indicate that none of the recognized taxa are polymorphisms of a lesser number of species.

TABLE I
MEANS OF FOREWING MARGIN MEASUREMENTS

Species Name	Sex	Sample Size	Mean Lengths			Three Margin Sum
			Costal Margin	Outer Margin	Inner Margin	
Catocala	M	9	19.2mm	11.8mm	15.6mm	
chelidonia	F	41	19.7mm	12.1mm	16.1mm	
	Species	50	19.5mm	12.0mm	15.9mm	47.4mm
Catocala	*M*	*38*	*19.4mm*	*11.8mm*	*15.1mm*	
a. benjamini	F	52	21.1mm	12.7mm	16.2mm	
	Species	90	20.3mm	12.3mm	15.7mm	48.3mm
Catocala	M	16	20.2mm	12.1mm	15.3mm	
californiensis	F	50	21.3mm	12.9mm	16.5mm	
	Species	66	20,8mm	12.5mm	15.9mm	49.2mm
Catocala	M	39	20.5mm	12.5mm	15.9mm	
a. andromache	F	46	21.2mm	12.9mm	16.5mm	
	Species	85	20.9mm	12.7mm	16.2mm	49.8mm
Catocala	M	36	20.3mm	12.4mm	16.0mm	
mcdunnoughi	F	28	21.9mm	13.5mm	17.4mm	
	Species	64	21.1mm	13.0mm	16.7mm	50.8mm
Catocala	M	16	21.5mm	12.3mm	16.6mm	
johnsoniana	F	13	22.5mm	12.7mm	17.3mm	
	Species	29	22.0mm	12.5mm	17.0mm	51.5mm

Wing Shape

To compare the differences in wing shape and proportions of the six taxa two types of data were used. The first was the means of the linear measurements of the wing margins given in Table 1. Comparing *chelidonia* with *benjamini,* while the costal and outer margins of *chelidonia* are shorter than those of the larger *benjamini,* the length of the inner margin of *chelidonia* exceeds that of *benjamini.* Thus the *chelidonia* forewing, by having a longer inner margin, must have an outer margin that is less oblique, altering the size of the apical and outer angles and making the wing more blunt. A close inspection of the wings of the two species confirms that the forewings of *chelidonia* are relatively broader and more blunt than the forewings of *benjamini.*

Comparing the mean length of the outer margin of *johnsoniana,* the largest species, with those of *mcdunnoughi, andromache andromache,* and *californiensis,* it is found that the outer margin mean length of *johnsoniana* is less than that of *mcdunnoughi* and *andromache andromache,* and equal to *californiensis.* The short outer margin of *johnsoniana* indicates the forewing to be relatively and actually narrower than those of the other three species. Again this is confirmed by examination of the specimens. As size differences between the species become limiting, the use of the linear measurements directly for further comparisons of the wing proportions of the species cannot be continued.

Wing Proportions

From species to species as wing shapes, angles, and proportions change, one would expect the wing margin lengths to change in correlated fashion. Accordingly, to eliminate the limitations on comparisons of wing shapes and proportions imposed by size differences, the original data, consisting of the linear measurements of the wing margins, were converted into ratios. Such ratios derived from the margin lengths should be similar for wings of the same shape and proportions. Two ratios were used: the first, the ratio of the costal margin length to the outer margin length; the second, the ratio of the costal margin length to the inner margin length. The ratios were converted into decimal values for each of the specimens used in the study and the species means determined. Finally, the species means of the two ratios were multiplied to yield a product of proportionality for each species. Thus a single value was obtained characterizing the forewing proportions of each species. It was found to be unnecessary to keep the data separate for the two sexes, as the ratios for both sexes of a species were quite the same. The proportionality data are presented in Table 2. The data are graphed in Figure 2.

Broad blunt wings should have comparatively long outer and inner margins. These, when divided into the costal margin lengths, should give low proportionality ratios. A comparison of *chelidonia* and *mcdunnoughi* with the other taxa discloses that ratios and products for both are lower than those of the rest. The differences in their products from the others are significant (P is less than .0001 for both.). The data confirm the resemblance between these two species first observed by Brower. The difference between *chelidonia* and *mcdunnoughi* is significant also (P equals .012).

Narrow wings with more oblique outer margins may be expected to have shorter outer and inner margins that yield larger ratios and products. We find that the ratios and products of the remaining four taxa are larger and representative of such wing shapes and proportions.

The proportionality ratios and products of *andromache andromache, andromache benjamini,* and *californiensis* have similar values, setting these three taxa apart as a middle group of species. The products of the three differ significantly from those of *chelidonia, mcdunnoughi,* and *johnsoniana* (P is less than .001 for all.). Among the three the product of *californiensis* differs significantly from both *andromache benjamini* and *andromache andromache* (P equals .007 and less than .001 respectively.). This confirms the distinctness of *californiensis* as a species from the other two. The difference between *andromache benjamini* and *andromache andromache* is not significant, supporting Bower's judgment in treating these two taxa as subspecies of a common species.

The costal margin-inner margin ratio of *johnsoniana* is equal to those of *andromache benjamini* and *andromache andromache.* But the costal margin-outer margin ratio and proportionality product of *johnsoniana* are the highest of the group and distant from the rest. These differences are highly significant.

TABLE II
FOREWING MARGIN PROPORTIONALITY RATIOS AND PRODUCTS

Species	Costal-Outer Margin		Costal-Inner Margin		Ratio Products	
	Ratio Mean	Standard Error	Ratio Mean	Standard Error	Prod. Mean	Standard Error
Catocala chelidonia	1.63	.0079	1.23	.0044	2.00	.012
Catocala a. benjamini	1.65	.0058	1.29	.0037	2.13	.0096
Catocala californiensis	1.66	.0066	1.31	.0045	2.17	.011
Catocala a. andromache	1.64	.0057	1.29	.0034	2.11	.0093
Catocala mcdunnoughi	1.62	.0066	1.26	.0040	2.04	.010
Catocala johnsoniana	1.76	.011	1.29	.0051	2.27	.017

Summary

Until sufficient material is available for a comparative study of the immature stages, generalizations about the relationships and phylogeny of the six taxa should not be attempted. However, this comparative analysis of the forewing sizes, shapes, and proportions indicates:

1. The distinctness of the populations of the six taxa, each having a characteristic mean size;
2. Measureable differences in wing proportions exist that can be characterized by numerical ratios and products useful for comparisons;
3. A group of two species, *chelidonia* and *mcdunnoughi,* with relatively blunt, broad wings;
4. A group of three taxa with moderately narrow and acute wings, *andromache andromache, andromache benjamini,* and *californiensis;*
5. A statistically significant difference between *californiensis* and the two *andromache* subspecies.
6. A close resemblance between the two *andromache* subspecies, the difference not being statistically significant;
7. A third group of one species, *johnsoniana,* with very narrow wings in proportion to their length, and the largest of the six taxa in size.

Acknowledgments: The authors express their thanks to Mr. Gordon Marsh, Museum of Systematic Biology, University of California, Irvine, to Dr. Charles L. Hogue and Mr. Julian P. Donahue and their staffs, Department of Entomology, Los Angeles County Museum of Natural History, for their assistance in securing needed publications, to Dr. A. E. Brower for identification of specimens, to Mr. and Mrs. Hugo Kinner for collecting privileges on their property, and to Mr. Ronald Leuschner for information on species distributions.

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Editors Note: One of the reviewers and myself were concerned with the matter of reference to the sympatric occurence of two subspecies, i.e., *andromache* and *benjamini.* The reviewer's comments were:

"If *andromache* and *benjamini* are subspecies, how could you have collected them in the same place? *Benjamini* is supposed to be an Arizona subspecies and should not occur within the range of nominate *andromache,* unless you were in some sort of blend or overlap zone. In general, if two things occur together and remain consistently distinct, they are species, not subspecies."

"A further comment on the subspecies problem. I do not understand how you could expect significant differences between samples of two "subspecies" collected in the same place. They should all be the same subspecies in southern California, unless *benjamini* is really just a color form that can occur anywhere. Its status may need to be reexamined."

Mr. Johnson answered these questions as follows, thus clariflying the matter:

"While *andromache andromache* is primarily a species of the coastal slopes of the Sierras and mountains of southern California, and *andromache benjamini* is a taxon of the desert slopes and Arizona, their ranges overlap and they have sympatry at points along the desert slopes of the high ranges of southern California. When Brower described *benjamini* from Arizona material, it was not known that *benjamini* populations existed in California also. I have sent a letter to Brower on Tuesday, October 23, 1979 calling his attention to the fact that in the zone of overlap there are no intergrades or hybrids, and that I have succeeded in rearing both species from ova to adult, finding that the ova and larvae are quite different. (These data being readied for publication now). In courtesy to Dr. Brower, who is preparing the *Catocala* volume for *Moths of North America,* I have left this designation of *benjamini* as a full species to him. In the present paper the wing proportion data of themselves do not support a change of *benjamini* to a full species, I have purposely avoided the change."

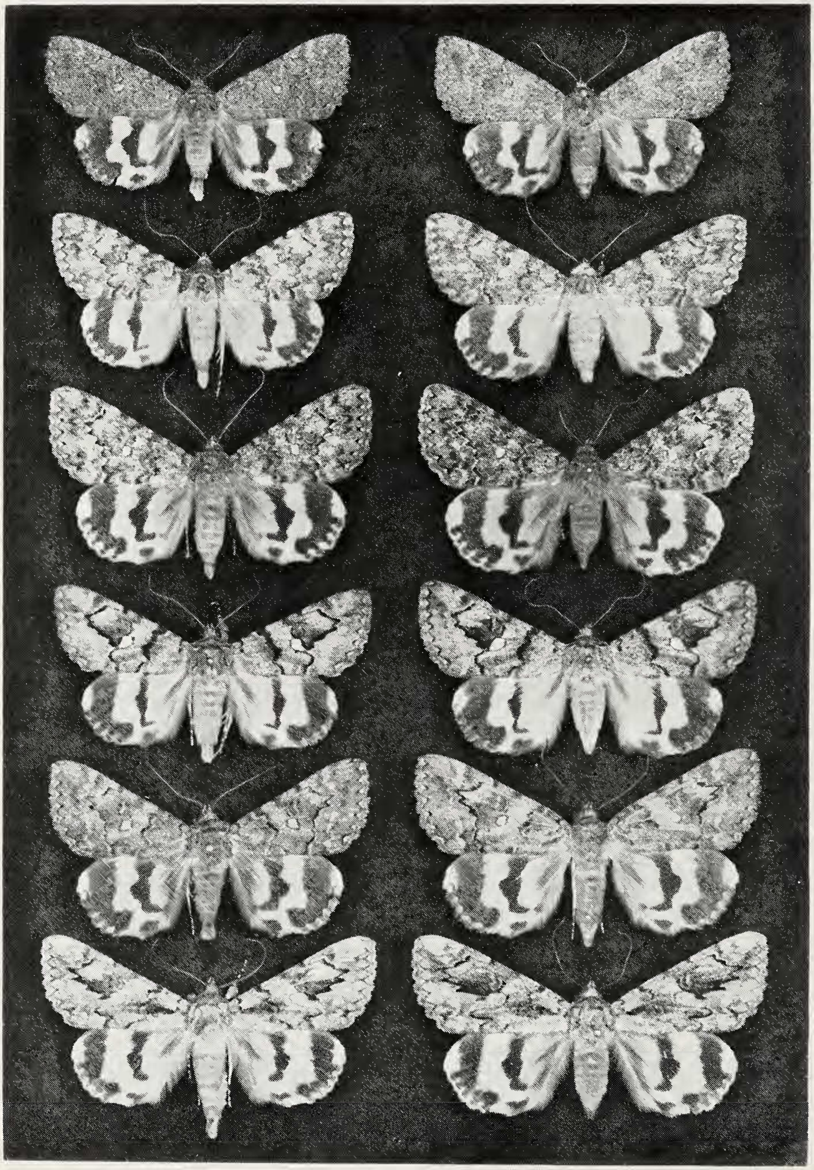

Figure 1. Pairs, male left, female right, from top downward, of: *Catocala chelidonia, Catocala andromache* subspecies *benjamini, Catocala andromache* subspecies *andromache, Catocala californiensis, Catocala mcdunnoughi,* and *Catocala johnsoniana.*

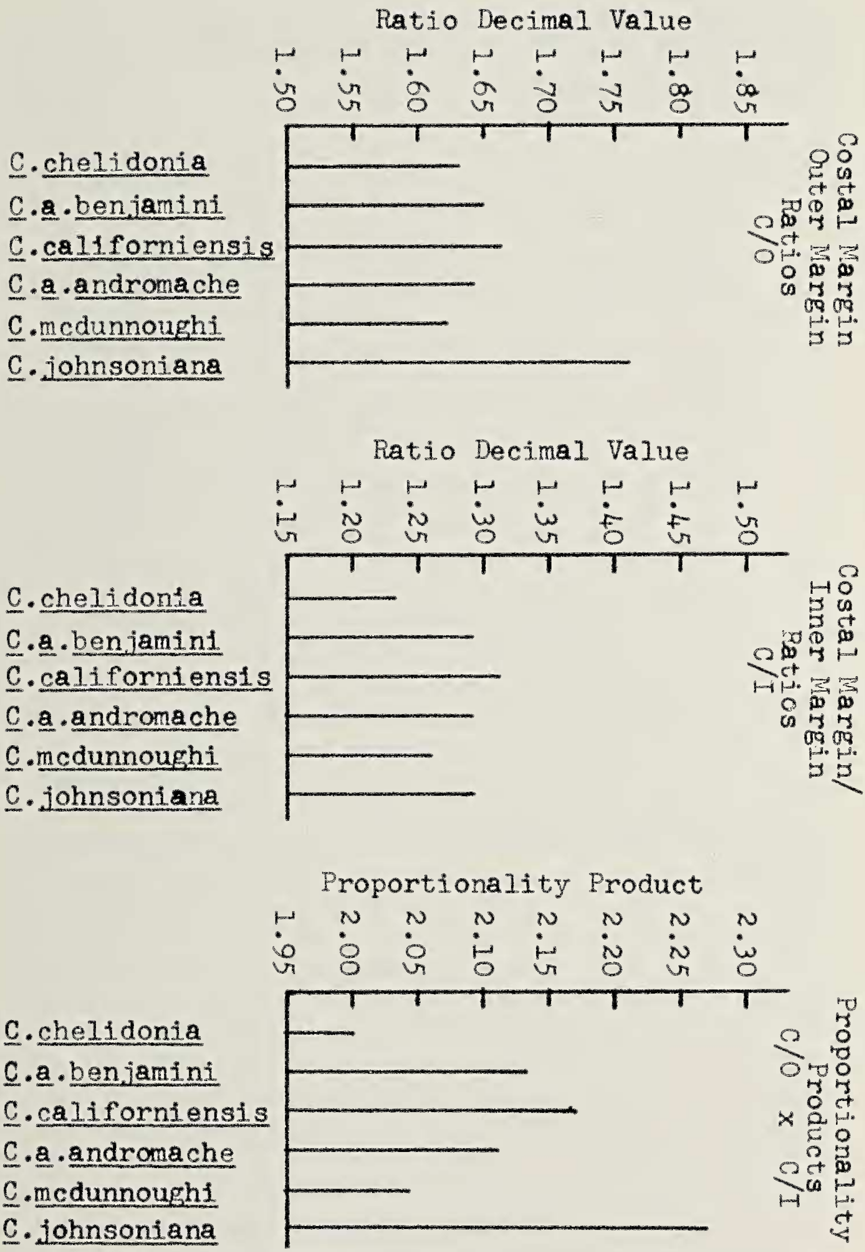

Figure 2. Graphs of Forewing Margin Ratio Decimal Values and Proportionality